

Resource Partitioning Among Colonies of Polygyne Red Imported Fire Ants (Hymenoptera: Formicidae)

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ABSTRACT Measurements of ant colony sizes and neighboring colony spatial structure figure importantly in a variety of socio-biological considerations. In this study, we used mass-marking and recapture techniques to quantify the foraging distribution and abundance of red imported fire ants, *Solenopsis invicta* Buren, on individual bait cards from neighboring polygyne (multiple queens) colonies. Ants in six to eight adjacent colonies, at each of 10 sites, were mass-marked a unique color. Ants were collected at olive-oil baits in a 10 by 10-m area consisting of 61 baits at each site. Stepwise nonlinear regression showed that the distance to baits, colony size, and average internidal (between nests) spacing were significant predictors of the foraging distribution of ants from colonies. Most marked ants were collected within ≈ 4 m of their colony. Foraging was more constrained at closer internidal distances. As internidal distances increased, colony foraging distances increased. There was a significant difference in the number of observed ants from colonies on individual baits compared with the expected number from the regression model. A χ^2 analysis showed that high numbers of ants on individual baits from a colony had a significant negative effect on the number of foragers from adjacent colonies. Results show $\approx 66\%$ of the variation in foraging can be explained through colony size, location, and recruiting ability; however, foraging interference among ants from adjacent colonies occurs and may result in unequal sharing of resources (i.e., resource partitioning) among colonies.

KEY WORDS *Solenopsis invicta*, red imported fire ant, polygyne, resource partitioning, foraging

RESOURCE PARTITIONING, THE DIVISION of shared resources, among ecologically similar ant species can reduce competition and lead to coexistence (Cerdá et al. 1998). Mechanisms of resource partitioning among different ant species are well documented and often occur through differences in aggressive abilities (Perfecto 1994, Bestelmeyer 2000, Andersen 1992), temperature preferences (Albrecht and Gotelli 2001), chemical defense (Andersen et al. 1991), caste polymorphism (Hölldobler and Wilson 1990, Detrain and Pasteels 1991), and territoriality (Levings and Traniello 1981). Resource partitioning among ant colonies of the same species often relies on measures of colony size (Herbers and Choiniere 1996, Holway and Case 2001), which generally bear a relationship to competitive ability and territory area (Adams 1990, 1998, Adams and Tschinkel 1995). However, the mechanism(s) of resource partitioning among ant species that do not aggressively defend resources from conspecifics are less understood. For example, polygyne (multiple queens) colonies of red imported fire ants, *Solenopsis invicta* Buren, do not engage in aggressive behaviors over resources (Vinson 1997). Pop-

ulation densities of polygyne *S. invicta* can be 2–10 times larger than monogyne (single queen) populations (Wojcik 1983, Macom and Porter 1996). This increased pest status can, in part, be attributed to the lack of nestmate recognition cues and reduced aggressive behaviors between conspecifics (Tschinkel 1998).

Although individual polygyne *S. invicta* and the colonies they comprise are significantly smaller and more numerous than their monogyne counterparts, the total amount of ant biomass estimated per unit of area remains significantly greater in polygyne situations (Macom and Porter 1996). Both social forms occupy and co-occur in similar habitats (Greenberg et al. 1992, Porter 1993), suggesting that foraging ability or resource use by polygyne *S. invicta* is an important factor in their success and ability to maintain such elevated colony densities and biomass.

There has been considerable research on resource partitioning (territoriality) of monogyne *S. invicta* (Adams and Tschinkel 1995, Adams 1998); however, there is little information quantifying polygyne resource use. Foraging of polygyne *S. invicta* has been qualitatively described as uniform and tenacious across an area, whereas monogyne foraging is thought to fluctuate more, both temporally and spatially (Bhatkar 1987, Bhatkar and Vinson 1987, MacKay et al.

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1994). Neighboring colonies of polygyne *S. invicta* have been referred to collectively as "supercolonies" with free exchange of food and workers among colonies (Vander Meer and Porter 2001). Previous studies by Drees et al. (1992) showed that spot applications of the toxic ant bait Logic (active ingredient: fenoxycarb) to the top of polygyne *S. invicta* mounds negatively impacted neighboring colonies. Drees et al. (1992) questioned whether the toxic properties of the baits were being "passed" through trophallactic (exchange of alimentary food) behavior among neighboring colonies, overlap in resource use among neighboring colonies, or multiple colonies competing on individual baits. Martin et al. (1998) examined the foraging range of polygyne *S. invicta*. Using insecticide baits, they created alternating strips of areas of reduced fire ant activity next to areas of normal ant activity (control areas). In the absence of competing ant colonies, they estimated the foraging distance of polygyne *S. invicta* to be ≈ 30 m in their "ant-free" strips. However, individual ants were not marked and tracked in this study.

Several ant and food marking studies have been used to determine foraging patterns and territory limits of imported fire ants (Bhatkar and Kloft 1977, Showler et al. 1989). Methods used for marking ants include food dyes, radioactive labels, rare earth elements, and paint marks (Paulson and Akre 1991, Weeks et al. 2004). In this study, a physical mass-marking technique was used to quantify the foraging distance and the degree and extent of resource partitioning of ants on food resources from several neighboring polygyne *S. invicta* colonies.

Materials and Methods

Foraging experiments were conducted in three old-field pastures with domestic cattle grazing in College Station, TX, and in a fourth field located behind the San Jacinto River Authority Dam in Conroe, TX (mowed monthly). Field sites were relatively homogeneous with respect to plant cover, soil characteristics, topography, and water drainage. Fields were separated by >1 km. Foraging behavior was examined in June, July, and August of 2000 and 2001. The experimental design consisted of 2–3 sites within each field (10 sites total) with 6–8 neighboring colonies as treatment mounds within each site ($n = 71$ colonies examined).

A mass-marking technique was used to mark ants in each colony a unique color (Bhatkar et al. 1991). Ants that came to the surface of a nest, after a brief period of light tapping on and around the nest, were painted a unique color. Testors Gloss Enamel paints (Zinc chromate 1184, Green 1124, Gray 1138, Red 1103, Orange 1127, Purple 1134, Blue 1110, White 1101, Testor Corporation, Rockford, IL) were applied with a small canister of compressed air using an inexpensive airbrush. Spray paints readily adhere to the lipid epicuticle layer of ants and are easy to distinguish under a $10\times$ microscope. Behavioral studies by Bhatkar et al. (1991) showed that this marking technique and com-

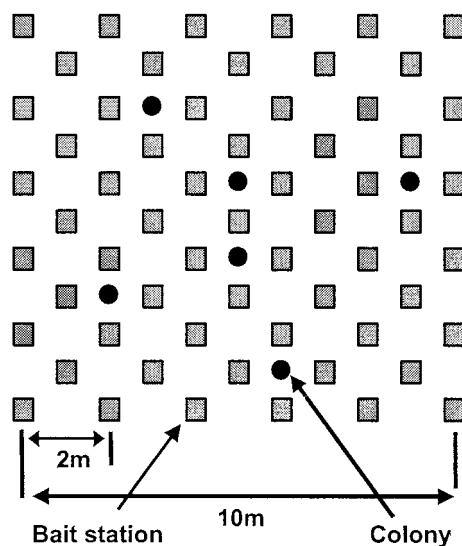


Fig. 1. Arrangement of 61 bait locations in 10 by 10-m area containing marked ant colonies.

bination of paints did not seem to affect ant longevity, behavior, nestmate, and/or non-nestmate recognition responses among painted and unpainted ants.

Ant foraging experiments were conducted 24 h after mass-marking. All foraging experiments were conducted during known ant foraging temperatures (25–30°C). High numbers of ants foraging on baits were detected in all foraging trials. Ants were collected at bait stations on 2.5-cm² olive-oil soaked index cards. Bait cards were placed inside a clear 50-ml polypropylene centrifuge tube (Corning, One Riverfront Plaza, Corning, NY). Bait tubes were wrapped in a fitted paper tube to reduce direct light exposure on the baits. In previous trials, baits that were left out in clear tubes, with no covering, had dirt and debris piled on them by the ants. This may be an adaptive behavior to bury and protect baits from UV radiation and discovery by other ants (Hölldobler and Wilson 1990). Baits in covered tubes eliminated this burying behavior and provided "clean" samples of ants on baits.

At each site, ants were collected at olive-oil bait cards in a 10 by 10-m area. Sixty-one baits were arranged at each sampling area (Fig. 1). Baits were placed flush with the ground surface for two consecutive foraging bouts of 45 min each. After 45 min, baits at a site were removed, capped, and replaced with another bait at the same locations for a second 45-min sampling period (90-min total sampling per bait location). Ants collected in both sampling periods were combined for each location. A total of 610 bait stations were sampled for 90 min of foraging activity per bait station, resulting in 54,900 min of foraging behavior.

At each site, all bait and marked colony locations were mapped to the nearest 5 cm. Following foraging trials, marked colonies at each site were excavated from the soil and placed in 18,900-ml plastic buckets lined with talcum powder and transported to the lab-

oratory for ant removal and biomass measurements. Ants in each colony were slowly "dripped-out" (Banks et al. 1981) of the soil with water and allowed to air dry. *S. invicta* is a flood-plain adapted species, which build living rafts of ants that can float on top of water (Hölldobler and Wilson 1990), which makes them easy to collect using this method. After soil extraction, ants and brood floated from colonies were anesthetized with CO₂ and weighed. Confirmation of the social form of the colony was made with an aggression bioassay conducted after colony excavation and dripping.

For the bioassay, aggression was examined using five ants randomly chosen from each colony (Obin et al. 1993). Colonies were paired individually until all colonies in a site were tested against each other. If there was no evidence of colony aggressive behavior (i.e., no biting or following) among the ants, it was assumed that the colonies were polygynous. If aggression was observed, colonies were classified as monogyne and excluded from the analyses.

Foraging Distribution. Stepwise least squares regression analyses and goodness-of-fit statistics were used to quantify the degree and extent of fire ant foraging from marked colonies. For the regression analyses, the dependent variable was the cumulative proportion of marked ants collected at increasing distances from each colony for each study site. The independent variables for the analysis were the distances from colonies to the food baits, estimated colony biomass, and the average distance between marked colonies for each study site (Equation 1).

$$\hat{Y}_{i,j,k} = 1 - \exp\left(\frac{-\beta d_{j,k}}{m^\gamma s^\theta}\right) \quad [1]$$

where, $\hat{Y}_{i,j,k}$ is the cumulative proportion of marked ants collected in the i th site for the j th colony at the k th foraging distance, ($i = 1-10$ sites, $j = 1-8$ colonies, and $k = 1-61$ bait locations), $d_{j,k}$ is the distance (cm) between the j th colony and the k th bait, m is the colony biomass (mg), and s is the average internidal distance (cm) between marked colonies. Constants β , γ , and θ were estimated from the data. The biological rationale for Equation 1 is dictated by the exponential increase in the area surrounding colonies that must be accounted for as the linear distance from each colony increases.

Model performance and the predictive ability of each independent variable were evaluated with a series of incremental F -tests. All tests for significance were evaluated at $\alpha = 0.05$.

Foraging Abundance. χ^2 statistics were used to determine if the observed abundance of marked ants on individual baits deviated significantly from the expected abundance of marked ants. The expected abundance was derived using Equation 1, which approximates the average foraging response of all colonies evaluated and assumes there were no behavioral mechanisms preventing ants from different colonies foraging on the same bait at the same time (overlapping). Some colonies were predicted to have more

ants on a bait than other colonies because of their closer proximity to the bait or larger colony size.

Foraging Superiority. The binomial probability distribution function (Bluman 2001) was used to calculate the expected number of numerically superior colonies on all baits, where n represents the number of colonies on a bait, k is the number of "numerically superior" colonies on a bait, and P is the probability of a numerically superior colony being on a bait. The expected frequency distribution assumed that colonies shared baits relative to their predicted foraging distributions and that the presence of ants from one colony did not influence the availability of the bait to ants from other colonies. Colonies were classified as numerically superior on a bait when the observed number of ants from a colony was greater than the expected number predicted by the regression model (Equation 1). A table of colony numerical superiority on each bait was constructed, and a χ^2 test was used to determine if there were any significant differences between the observed and expected frequency classes of the number of numerically superior colonies on baits. For example, for the observed data, on bait 2 at study site 1, if one colony had more marked ants collected on that bait than expected, whereas the other six colonies had fewer ants than expected, that bait would be assigned to the class frequency of one-sixth; meaning one colony was numerically superior, whereas six colonies were under-represented. The observed frequency distribution of the superiority scores (0/7 through 7/0) was compared with an expected distribution.

Results

Of the 71 colonies that were studied, nine did not contribute marked ants on baits. An additional nine colonies were excluded from the analyses after the aggression analyses suggested they were monogyne colonies. This left 53 polygyne colonies for analyses. A total of 282,807 ants were collected from the 610 bait locations, with 17,615 (6.23%) being marked. Of the 610 baits, 272 did not have marked ants; however, only 30 baits failed to collect any ants. Of the 30 baits that did not have any ants collected, 25 were from the two Conroe sites. The grass was taller in these sites compared with the other sites, suggesting that baits may take a longer time to be discovered in areas with tall vegetation. Also, in one of the Conroe sites, a native ant, *S. geminata* (Fab), was collected at two bait stations.

The mean \pm SD internidal distance among all nests was 128.9 ± 88.3 cm for the first nearest neighbor, 192.3 ± 66.9 cm for the second nearest neighbor, and 223.2 ± 57.4 cm for the third nearest neighbor. These distances were similar to polygyne internidal distances measured in a previous study (Bhatkar and Vinson 1989). Colony sizes ranged from 1,280 to 39,370 mg (mean, 9,869 mg).

Foraging Distribution. Parameter estimates and goodness-of-fit statistics for the stepwise regression models are presented in Table 1. Results from the

Table 1. Stepwise nonlinear regression goodness-of-fit statistics for quantifying the foraging distribution of polygyne *S. invicta*

Number of parameters ^a	Model constants				Goodness-of-fit statistics				
	β	γ	θ	R^2	SSE	SSM	Total	df numerator	df denominator
1	0.0060	0.000	0.000	0.639	15.281	27.087	42.368	1	538
2	0.0185	0.1276	0.000	0.648	14.897	27.471	42.368	1	537
3	0.3219	0.1260	0.468	0.657	14.520	27.848	42.368	2	536

^a Refers to the number of parameters retained in the foraging prediction model.

$\hat{Y}_{i,j,k} = 1 - \exp\left(\frac{-\beta d^{1/k}}{m^{\gamma} s^{\theta}}\right)$ in Equation 1. See text for a description of the parameters.

incremental *F*-ratio tests show that the three-parameter regression model was significantly better at explaining ant foraging distribution compared with the single or two-parameter foraging model (Table 2). The three-parameter regression model shows that the distance between a colony and a food source, colony size, and the average distance between colonies explained $\approx 66\%$ of the variation in the foraging distribution of ants from marked ant colonies (Table 1). The influence of each parameter estimate on the foraging model is shown in Fig. 2a and b. Figure 2a shows the predicted cumulative proportion of marked ants collected from a colony as a function of distance to food baits and estimated colony size (largest, average, and smallest). Large colonies have a significantly higher foraging potential at nearly all distances compared with smaller colonies (Fig. 2a). For example, at distances ≥ 400 cm, large colonies can get proportionately more ants on a bait and correspondingly have more foragers available to go farther distances compared with a smaller colony at the same distance. Figure 2b shows the predicted cumulative proportion of marked ants collected as a function of distance to food baits controlling for internidal spacing (largest, average, and smallest). Figure 2b also shows that the average distance between colonies in an area significantly constrains foraging for all colonies in that area. The smaller the average distance between colonies (closer spacing) the more foraging is constrained. Conversely, the larger the spacing between nests the less constrained foraging becomes (Fig. 2b).

Foraging Abundance. While the foraging equation captured the effect of distance on colony foraging, it did not explain the abundance of foragers on individual baits well. Ninety-seven percent (328) of the 338 baits with marked ants had significant χ^2 statistics, indicating that most baits had either significantly more

or less marked recaptures from individual colonies than predicted by the foraging equation.

Foraging Superiority. The binomial probability distribution function was used to calculate the expected number of numerically superior colonies on all baits. If the presence of a numerically superior colony on a bait can be defined as a random phenomenon, *P* would equal 0.5. The least-squared deviation estimate for *P* showed significant departure from random expectation with *P* = 0.194. χ^2 analysis shows that the frequency distribution of observed numerically superior colonies was significantly skewed to a few numerically superior colonies ($\chi^2 = 88.27$, *k* = 30–1, *P* < 0.001, where *k* is the number of frequency classes of numerically superior colonies). Regardless of the number of ant colonies found foraging at a bait, there were significantly more baits than expected with one numerically superior colony and significantly fewer baits found with zero, two, or more numerically superior colonies (Fig. 3). Of the 53 colonies used in this anal-

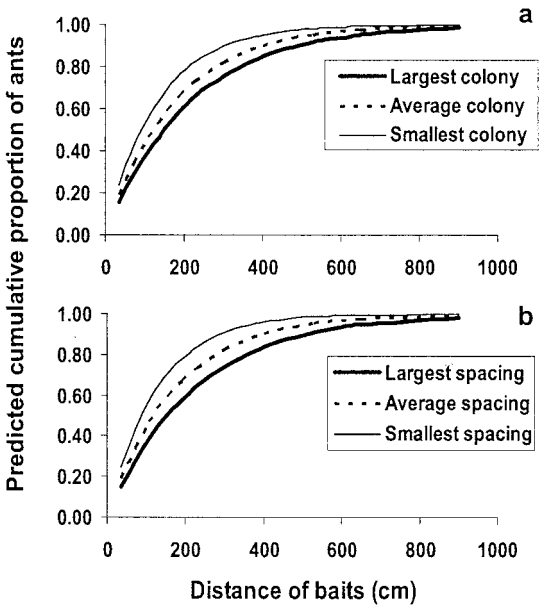


Fig. 2. Predicted foraging distributions by (a) colony size controlling for internidal distance (458 cm = average observed) and (b) internidal spacing controlling for colony size (9,869 mg = average observed).

Table 2. Incremental *F*-ratios comparing the costs and increased predictive ability of parameter inclusion in the stepwise regression models describing the foraging distribution of polygyne *S. invicta*

Parameter comparisons	<i>F</i> -ratio ^a	df numerator (respectively)	df denominator (respectively)
Model 1 versus Model 2	13.84 ^a	1, 1	538, 537
Model 2 versus Model 3	8.97 ^a	1, 2	537, 536

^a significant *F*-ratio > *P* = 0.05.

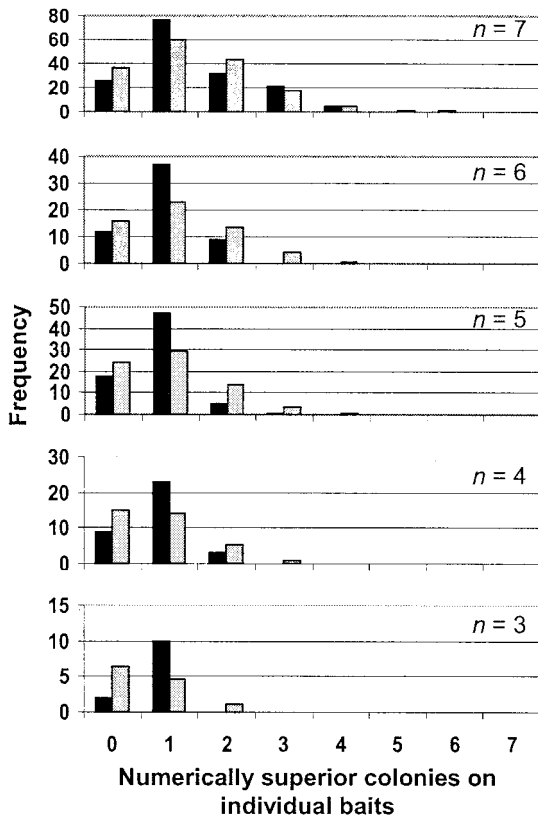


Fig. 3. Frequency distribution of the number of numerically superior colonies individual baits. Note scale differences among graphs. n is the number of colonies represented on baits. ■, observed; □, expected.

ysis, all were numerically superior on at least one bait. The overall mean \pm SD number of baits at a site with numerically superior numbers of ants from a colony was 6.41 ± 3.12 .

Discussion

This study, on resource use patterns among colonies of polygyne *S. invicta*, relied on mark and recapture techniques and simple colony variables such as colony sizes, numbers, spacing, and locations that are commonly estimated in field studies. In this study, most of the foraging around polygyne colonies (>90%) occurred within ≈ 4 m from the colony, indicating that foraging is localized around the nest. Colonies responded, to the best of their numeric ability, to the foraging relationships present among its neighbors. Short internidal distances force colonies to commit more of their foragers to resources closer to the colony compared with situations where internidal distances are greater and colonies can successfully forage in a larger area. Variation in the degree of resource partitioning among co-existing colonies, at high densities, is related to the ability of one or more colonies to get numerically superior numbers of ants on baits to the

reduction of foragers from other colonies. This is the first record of such resource partitioning in polygyne *S. invicta*. Similar mechanisms of resource partitioning and interference competition along body/colony size have been shown in a variety of taxa (e.g., lizards and birds, Schoener 1974; ants, McGlynn 1999; ant colonies, Holway and Case 2001). In this study, ants acquired some resources through limited overlap on baits. However, no data were collected on limiting resources or colony fitness costs related to interference foraging/competition.

Polygyne *S. invicta* are not aggressive to non-nest-mates, and aggressive behavior was not observed among ants on baits. This suggests that behavioral aggressive confrontations on baits were not responsible for the observed patterns of resource partitioning and reduced overlap of foragers from adjacent colonies on baits. Resource use by polygyne *S. invicta* may be adaptive in supporting elevated levels of ant colonies and biomass where food resources are quickly secured through rapid and overwhelming recruitment among competing colonies of the same and/or native species. Under this adaptive nonaggressive foraging strategy, colonies must be fast at finding and recruiting ants to food sources; otherwise, they may be outcompeted by another colony in the area. With this foraging strategy, food resources are seldom "locked-up" and held exclusively in a territory, as in the monogyne scenario, but rather at a specific point in time some food resources are shared, to a limited extent, with other colonies, while food resources not being used by one colony are available to another neighboring colony. In a study of food flow among neighboring polygyne *S. invicta*, Weeks et al. (2004), using rare earth elements, showed that, in addition to distance to food resources and colony size, food type (lipids, protein, carbohydrates) and life stage (adults, larvae) of ants were significant predictors of food distribution patterns.

Food size is assumed to be an important determinant of foraging overlap on resources and the distribution of food resources. In this study, a bait size of 2.5 cm² was used, which was large enough to allow for more than a single colony to be represented on it. Smaller food sizes will reduce or eliminate overlap of foragers among colonies, whereas larger food sizes may require partitioning among colonies relative to their recruitment abilities.

Although polygyne *S. invicta* share, to a limited degree, food resources, heterogeneity in recruitment abilities and resource distribution patterns may arise through differences among colonies in their respective biomass, demography, location, relative nest density, resource consumption abilities, and internal dynamics. Foraging interference may occur in locations where the foraging potentials of two or more colonies significantly overlap. Resource partitioning on baits is likely the result of additional factors, such as fast recruitment ability related to extensive foraging tunnel networks and the location and size of food resources relative to colony and tunnel locations. Localized foraging areas among polygyne colonies may be delin-

ited by the network of foraging tunnels used by ants (Zakharov and Thompson 1998). Zakharov and Thompson (1998) showed the foraging tunnel network of several neighboring polygyne *S. invicta* colonies were highly branched and terminated within ≈ 4 m of the colony.

Quantitative data on spatial and temporal dynamics of polygyne *S. invicta* foraging behavior can be used to better understand their pest status, levels of social organization, resource use, and patterns of pathogen transfer among colonies. This research provides data that suggests that polygyne *S. invicta* colonies do not share food resources equally and frequently engage in interference foraging on food baits. Once a polygyne colony becomes established, just as monogyne colonies, it must quickly grow large enough to compete against its neighbors for foraging space and resources. Unlike monogyne colonies, polygyne colonies do not compete for resources through aggressive encounters, but rather they partition resources relative to their size and place within the surrounding community of colonies.

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